

## Locomotor Ecology of *Lepilemur edwardsi* and *Avahi occidentalis*

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**ABSTRACT** A well-known principle holds that where food supply is limited, two sympatric species with the same diet, morphology, and behavior will compete, leading to exclusion of one species or differentiation of their ecological niches. *Avahi occidentalis* and *Lepilemur edwardsi* are two saltatory, nocturnal folivorous lemurs of similar body size which live sympatrically over much of their range and may often be seen feeding in the same trees. We report a study of their locomotor behavior, carried out in order to determine to what extent locomotion might contribute to niche separation. *Avahi* lives at a higher level in the forest and is the more committed leaper, with a much larger home range and nightly travel distance, while *Lepilemur* climbs more and has a very small nightly travel distance. *Avahi* uses small, low-angled supports more often, while *Lepilemur* makes more use of large, high-angled supports (however, neither species uses vertical supports at a frequency greater than the availability of such supports in the forest stratum in which they live). Both species tend to land on larger-diameter supports on longer leaps, but *Avahi* also takes off from larger-diameter supports in longer leaps, reducing loss of energy to the substrate during takeoff. We suggest that the differences in locomotion and ranging behavior between them are consistent with niche differentiation on the basis of food quality, *Avahi* investing more energy in harvesting better quality but more patchy food, *Lepilemur* minimizing expenditure in harvesting a less selective, quantitatively poorer diet. *Am J Phys Anthropol* 104:471–486, 1997. © 1997 Wiley-Liss, Inc.

When two species with similar activity pattern, diet, and body size live in sympatry and food availability is limited, we may expect that niche differentiation or competitive exclusion will occur (Hutchinson, 1957; Pianka, 1974 and see e.g. Charles-Dominique, 1977). *Lepilemur edwardsi* and *Avahi occidentalis* are nocturnal folivores of around 900–1,000 g mass which both occupy the deciduous Western Dry Forest of northern Madagascar. In the Western Dry Forest, many trees become nearly bare of leaves during the dry season, and seasonal food shortages may be expected to exert a strong

selective pressure (Hladik, 1980). In the forest of Ankarafantsika, *Lepilemur* and *Avahi* have at least three potential competitors: *Propithecus verreauxi coquereli*, *Eulemur fulvus*, and *Eulemur macaco*. *Microcebus murinus* and *Cheirogaleus medius* are also sympatric with our subjects. The latter

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witnesses to the existence of seasonal food shortages by its hibernation during the dry season.

Not only are *Lepilemur* and *Avahi* unusually small for primate folivores, sitting astride Kay's threshold (Kay, 1984), but they are also unusual in combining folivory with nocturnality, so that they harvest their major resource at a time in which it is likely to be low in available sugars (Martin, 1990). Anywhere else except Madagascar, we would also be surprised to see folivory combined with a primarily saltatory (Walker, 1979) locomotion. Since leaping is acyclic, it usually lacks opportunities for energy conservation; elastic storage of energy in tendons is available primarily to large-bodied mammals where tendon cross-section is greater (Biewener et al., 1981; Alexander, 1991), and leaves are an energy-poor reward for the energy invested in locomotion during foraging. Specialist saltatory species outside Madagascar tend to take much richer food: sugar-rich gums, fruit, and sap, augmented by insects in the case of *Galago moholi* (Crompton, 1984) and protein-rich animal prey in the case of *Tarsius bancanus* (Crompton and Andau, 1986), for example. Indeed, Charles-Dominique and Hladik (1971) have gone so far as to claim that *Lepilemur leucopus* balances its energy budget partly by coprophagy, although their claim has been challenged by Russell (1975) on the basis of data from another part of the same fieldsite, and the claim has not since been repeated. Russell (1975) further denied Charles-Dominique and Hladik's claim that *Lepilemur leucopus* was also characterized by low levels of activity, but Nash's (in press) study of *L. leucopus* tends to support Charles-Dominique and Hladik (1971) in this respect. She further demonstrated that inactivity levels increased in periods of thermoregulatory stress. While Nash (in press) has also quantified support use in *L. leucopus*, little quantitative data is available on the locomotor behavior of either *Avahi* or *Lepilemur*, although Albignac (1981a,b) provided ecological data on both *Avahi occidentalis* and *Lepilemur edwardsi* at Ampijoroa, while Razanahoera-Rakotomalala (1981, 1988) has examined aspects of their dietary behavior and Harcourt (1987, 1991) has carried out

comparable studies of *Avahi laniger* at Ranomafana.

More particularly, Ganzhorn (1993) has recently shown that leaves eaten by *Lepilemur* at sites where *Avahi* is present are of lower quality than those *Lepilemur* consumes at sites where *Avahi* is absent, indicating that *Lepilemur* has reduced the breadth of its niche in response to competition for younger leaves from *Avahi*. However, his finding that no difference exists between the species in the stratum occupied contrasts with other studies on prosimians: the classic study of sympatric lorises at Makoukou, Gabon, by Charles-Dominique (1977) showed that dietary differentiation can lead to differences in both stratum occupied and locomotor behavior. Crompton (1984, 1989) also found stratum, locomotion, and diet to be closely linked in *Galago*, while Nash et al. (1995) have found a linkage between diet and stratum in both *Galago* and *Lepilemur*. If true, Ganzhorn's (1993) finding that no difference exists in the stratum occupied by *Lepilemur* and *Avahi* at Ampijoroa suggests that their locomotor behavior should be very similar or indistinguishable, a conclusion which also might be expected from their similarity in body size and general *bauplan*.

The present paper reports a study of the locomotor behavior of *Avahi occidentalis* and *Lepilemur edwardsi* carried out at Ampijoroa, in the forest of Ankarafantsika. Together with studies of support preferences (Warren, 1997), ranging and social behavior (Warren and Crompton, in press a), and energy costs of locomotion (Warren and Crompton, in press b), our goal is to determine to what extent locomotor behavior, in its broadest sense, may contribute to niche separation as a response to competition for seasonally scarce food resources.

## METHODS

The field work took place between May 1992 and October 1993 in Jardin Botanique A of Ampijoroa Strict Forest Reserve, Majunga Province, Madagascar. Jardin Botanique A lies on a flat plateau with sandy soil. The dry deciduous pole forest has a canopy stratum at about 7–10 m high. A shrub layer is also present, and abundant

lianas are found at most levels (Ramangason, 1986, 1988).

A grid of surveyed markers was laid out, without cutting, in an area where both *Avahi occidentalis* and *Lepilemur edwardsi* were known to have sleeping trees. Four *Lepilemur edwardsi* and four *Avahi occidentalis* were captured, usually mid-morning, within the quadrat. No UK regulation covers the handling of animals in other countries, but handling methods were agreed in advance with the Department des Eaux et Forêts of the government of Madagascar and with the Commission Tripartite. The *L. edwardsi* were caught by noosing at their sleeping holes. An intramuscular injection of 0.1 ml of ketamine hydrochloride was given to facilitate handling of this quite aggressive species. The *A. occidentalis* were caught using either a blowpipe or an air gun (Telinject, Alsace, France) to propel darts (Distinject, Zurich, Switzerland) loaded with 0.2 ml ketamine hydrochloride (only part of this dose was found to be injected by the darts). The animals were rehydrated regularly by mouth, and full recovery occurred within an hour, so that animals were held for a maximum of 1.5 h. Each individual was weighed, and morphometric data were taken on body weight and segment lengths and diameters. A permanent ear notch was made for future identification. Each animal was fitted with a back-mounted transmitter (Biotrack, Wareham, UK). The transmitters each had a unique frequency and gave a range of about 120 m under the study conditions. They were sewn onto a leather base, coated with dental acrylic, held by a parachute-type harness of soft Teflon ribbon, and fastened with a rivet. The whole assembly had an average mass about 3% of that of the subjects. The choice of a backpack collar was made since we believe that neck-mounted collars are not acceptable for biomechanically oriented locomotor studies of leaping species, as they drastically alter the position of the body center of gravity; both species could remove a waist-mounted transmitter.

The subjects were located at their sleeping site (holes in trees for *L. edwardsi*, sleeping "huddles" in the low canopy for *A. occidentalis*) and followed whenever possible from the onset of activity until they

reached their sleeping site for the next day. Minimum nightly travel distances and ranges were measured using Crompton and Andau's (1987) technique; these are discussed in more detail elsewhere (Warren and Crompton, in press a). Red-filtered halogen caving lamps proved unable to illuminate the upper canopy sufficiently. Since the animals did not avoid white light and could be approached as close as 5 m when it was in use, we employed low-level white light when close to the subject, high-power illumination being reserved for locating the subject from a distance.

As Dagosto (1994) observes, recording observational data using instantaneous time sampling (ITS) approaches is not suitable when events are rare and unpredictable, as are locomotor displacements—in particular, of course, leaping. These problems are greatly augmented when studying small, nocturnal species, since continuous visibility of the subject over extended time periods is highly unlikely under field conditions and even less likely in closed environments. Bout sampling (Fleagle, 1978; Crompton, 1983; Doran, 1992; Dagosto, 1994), or in other words *ad libitum* recording, was therefore employed for observations of locomotion according to the schedules in Tables 1 and 2. An observation was recorded each time there was a change in the locomotion or behavior (i.e., an observation or activity bout started and ended with a change in behavior), but if a change of activity took place without pause, this was noted.

No particular sampling regime was adopted with respect to selection of individuals to be followed, but at least four all night "follows" were made on each individual, with a total of over 560 h of observations over an 18 month period. Postural behavior is much more amenable to measurement by ITS, but perhaps the most appropriate parameter may be time duration. In practice, however, it is difficult enough, even with radiotracking, to track small, saltatory nocturnal species sufficiently closely to allow a reasonable estimate of distance travelled, while simultaneously recording locomotor bouts, without attempting to use a stopwatch as well! For this reason, although postural behavior was

TABLE 1. Brief definitions of the locomotor categories

Locomotor mode	Definition
Sitting	The animal is stationary and supported under the rump by a branch
Standing	The animal is stationary and upright on its hind limbs
Clinging	The animal is stationary and upright, holding onto a vertical or angled support with both fore- and hind limbs
Leaping	Locomotion in which the animal jumps across discontinuities using an extension of the hind limbs
Climbing	Quadrupedal locomotion where height is gained or lost by moving up or down a single support which is vertical or angled
Walking	Quadrupedal locomotion where at least three limbs are in contact with a substrate which has an oblique or horizontal orientation
Foliage-crossing	Quadrupedal locomotion where the animal reaches across a gap to grasp foliage with one hand and then slowly moves the other limbs across one at a time
Cantilevering	Holding on to the substrate with a pair of limbs only and leaning across a gap to grasp another support
Frog-hopping	Jumping along the same support with the forelimbs as well as the hind limbs in contact with the support at the beginning and end of the leap
Kangaroo-hopping	Jumping along the same support with only the hind limbs in contact with the support at the beginning and end of the leap
Running	Fast quadrupedal locomotion where only two limbs are in contact with a support, which is oblique or horizontal.
Ladder-climbing	Climbing up or down a number of supports of any orientation using the supports like rungs of a ladder

recorded, we do not examine it in the present report.

The incidence of locomotor activities (defined in Table 1), their bout length (i.e., the estimated distance travelled horizontally, if any), the estimated height at the beginning and end of a locomotor bout, and the estimated diameter and angle of the initial and terminal supports were recorded, along with

TABLE 2. Schedule of locomotor observations

1	Date
2	Animal species and identification number
3	Time
4	Locomotor/postural mode
5	Initial support diameter: tiny (0 to <0.5 cm); small (0.5–5 cm); medium (5.1–10 cm); large (10.1–15 cm); enormous (15+ cm)
6	Initial support orientation: vertical (81–90°); angle (46–80°); oblique (11–45°); horizontal (0–10°); fork (two or more large supports); foliage (multiple fine supports)
7	Terminal support diameter (cm)
8	Terminal support orientation (see 6)
9	Initial height (m)
10	Terminal height (m)
11	Horizontal distance travelled (m)
12	Activity: rest; travel; feed; autogroom; allogroom; other
13	Continuous from previous observation (yes or no)
14	Number, direction, and distance of calls of the same species
15	Position of feed tree

the time at which activity occurred (Table 2), and any feeding or social behavior was also recorded. Point-to-point distances were also recorded (Warren and Crompton, in press a), and the data collection schedule was designed to be, as far as possible, directly comparable to that of previous work by Crompton (1980, 1983) and Crompton and Andau (1986). Considerable self-training in estimating heights, diameters, and distances between trees was performed during daylight hours. The data were recorded on cassette tape and then transcribed the following day into notebooks. A total of 3,405 locomotor bouts were retained for analysis for *Lepilemur edwardsi* and 3,375 for *A. occidentalis*.

### Statistical testing

Statistical testing of cross-species comparisons of locomotor data derived from observational fieldwork is beset with problems. Firstly, the unbalanced and "messy" nature of most datasets reduces the number of statistical tests which can be performed without violating the assumptions of the test. Secondly, many tests may be performed on the same data. In this case, significance levels will be cumulative, so that where a first test on a dataset gives a probability of .05, the second will effectively give a probability of .05 + .05 and so on. Thirdly, there is a problem of autocorrelation between locomo-



tor bouts performed by any given subject, which may effect the validity of species comparisons based on analysis of sequential bouts of individuals.

Boinski (1989) used arc sine transformations to correct for nonnormality of some variables and attempted to address the problem of autocorrelation by pooling data for individuals when comparing the proportion of time spent in each behavior. Fontaine (1990) compared means of the percentage contributions that given behaviors made to pooled data for individuals, and Gebo and Chapman (1995) gave alternative statistical comparisons, firstly comparing profiles of 100 sequential bouts, which were regarded as independent, and secondly comparing only every second set of 100 bouts. Dagosto (1994) provided a more extensive review of several of these problems and chose to address them by deriving test statistics from permutations of her datasets, using randomization statistics (e.g., see Manly, 1991; Edgington, 1987) to test her data, and by examining the number of individuals as the sample size. This is the most conservative of the approaches to the problems outlined above.

We have adopted a pragmatic approach, which provides both more liberal and more conservative assessments of our data, while utilizing only tests which are available in the two popular statistical packages, SAS and SPSS.

First, we address the problem of assessing an unbalanced dataset, while ignoring the problem of interdependence of sequential bouts of individuals, by using a general linear model (GLM) to look for species differences in continuous variables such as support diameter, changes in height, or distance travelled during various locomotor behaviors. This method avoids problems arising from unequal sample sizes (Milliken and Johnson, 1992), since GLM compensates for unequal numbers of observations for the different combinations of "class" variables (such as species and locomotor mode) in the model statement. A type III hypothesis was used to calculate sums of squares, and F ratios with their degrees of freedom and probabilities were derived. Least mean squares were calculated within the GLM

procedure along with the corresponding standard errors. Since the primary role of the GLM was to identify any unexpected distinctions between the species, we assumed that comparisons between classes were unplanned comparisons and tested them using Scheffé's test (as recommended in Milliken and Johnson, 1992).

Secondly, we provide the result of the same GLM model applied to means for each parameter for each individual, which also removes the risk from interdependence of sequential bouts. This provides the most conservative assessment of our data.

Thirdly, we provide species comparisons based on randomized 25% and 50% samples of the dataset (SPSS SAMPLE). These provide a more liberal assessment of our data than our second method but may to some extent reduce the problem of interdependence of sequential bouts of behavior by one individual by reducing the likelihood of sequential data for given individuals being included in the test sample. Statistically significant differences were identified using various parametric and nonparametric statistics as appropriate: *t*-tests, oneway ANOVAs, the Mann-Whitney U statistic, and cross-tabulations, using various measures of strength of association as well as chi-square statistics. Since the random sampling method does not eliminate the problems arising from unbalanced data, wherever possible we utilized exact tests provided by SPSS (SPSS EXACT) for use where data are unbalanced or sparse. These tests may be regarded as, in essence, randomization tests. Where the size of our dataset together with limitations of computer memory prevented us from using exact probability levels of the test statistic based on its exact distribution, we obtained an unbiased estimate of the exact significance probability using the Monte Carlo sampling method. This technique repeatedly samples from a reference set of tables with the same dimensions and row and column margins as the observed data (again using SPSS EXACT). Both methods are preferable to the usual asymptotic estimates of probability which assume that the data conform to a particular distribution and should also reduce the error arising from

TABLE 3. General linear model (GLM) test of significance between species for each variable, full dataset<sup>1</sup>

Locomotor mode	Diameter of first support	Diameter of second support	Height of first support	Height of second support	Equal height and height lost	Height gained	Horizontal distance
Leap	<.01	<.01	<.01	<.01	<.01		<.01
Climb	<.01	<.01	<.01	<.01	<.01		<.01
Walk			<.01	<.01			
Foliage			<.01	<.01			<.05
Cross							
Cantilever							
Frog hop	<.01	<.01	<.01	<.01			
Kangaroo hop							
Other	<.01						
Run							
Ladder							
Climb							

<sup>1</sup> Equal height and height lost refers to the vertical distance maintained or lost in a locomotor bout. This was separated from height gained to aid locomotion energy cost calculations because gaining height (and hence doing work against gravity) is more expensive than sustaining or losing height. Height gained is the vertical distance gained in a locomotor bout. Horizontal distance is the horizontal distance covered in a locomotor bout.

analysis of unbalanced data. Where the 25% sample gives significant differences, which are maintained for larger samples, results for the latter are not reported. In order to reduce error arising from cumulative probabilities over repeated tests, we treat probabilities of .05 or less as suggesting that differences may exist, probabilities of .01 or less as clear indication of a trend to difference, and the higher critical level of <0.005 as fully significant. We use the Mann-Whitney U statistic, which is described by Manly (1991) as essentially a randomization test of ranked data, conservative with respect to probabilities, as a check on *t*-tests and ANOVAs. We present our results in tables as fully as possible to permit assessment by other techniques if the reader prefers.

Finally, since raw horizontal distance is not the most appropriate measure of examining the mechanical relationship of leap length to support variables, we calculated, from the complete dataset of leaps, the mechanically effective leap length  $X_e$ , which is the maximum possible length of a level jump with the same takeoff speed. This takes into consideration height loss or gain. We assumed a 45° takeoff trajectory, which optimizes for mechanical energy costs. The equation used was  $X_e = (r \cos^2 \alpha) / (1 - \sin \alpha)$ , where  $\alpha$  is the angular displacement from the horizontal of the endpoint of the leap and  $r$  is the horizontal distance in meters (Crompton et al., 1993). Distances were re-coded into classes, and the mean initial and

terminal support diameters and height change were compared between classes using Duncan's multiple range test. Height change is of course used to calculate  $X_e$ , but in support of our findings we provide values for the correlation of raw length of leaps with height change.

## RESULTS

Unexpected differences were identified using a GLM of the whole dataset (Table 3). However, when the same GLM model was applied to a dataset comprised of the mean values for these parameters in each locomotor mode for each individual, there were only 69 cases (i.e., mean values for each individual), and, while values for the different locomotor modes were significantly different within species ( $P = .0001$ ), species differences were not significantly different.

We then derived descriptive statistics for our data, which are given in Tables 4–11 and highlighted, with statistical tests where appropriate, below.

### Locomotor mode frequencies

From the 25% sample, *Avahi* leapt considerably more (69.7% vs. 55.8% of locomotor bouts) but climbed considerably less (19.2% vs. 30.5%) and walked a little less (5.5% vs. 7.9%). Of the rarer modes, foliage-crossing was commoner in *Lepilemur* than *Avahi* (2.9% vs. 1.1%), and so was frog-hopping (2.2% vs. 1.5% of locomotor bouts). Other modes were less than 1% of displacements.

TABLE 4. The frequency of locomotor modes of *L. edwardsi* and *A. occidentalis*

Locomotor mode	<i>Lepilemur edwardsi</i> (%)	<i>Avahi occidentalis</i> (%)
Leaping	55.1	66.2
Climbing	30.3	17.6
Walking	7.5	6.3
Foliage-crossing	3.8	1.7
Cantilevering	0.1	0.8
Frog-hopping	1.8	1.6
Kangaroo-hopping	0.2	0.6
Other	0.5	0.8
Running	0.6	2
Ladder-climbing	0.1	2.4

The Pearson chi-square was 39.309, with an asymptotic significance of .00000, and Phi and Cramer's V was .18973 (memory was insufficient to perform exact tests, but the approximate significance was .00000). While probability levels are clearly significant, it should be noted that even when the full dataset was used, Lambda, a measure of association, did not give an improvement on predicting locomotor modes when species are known greater than 10%.

#### Contribution of locomotor modes to each kilometer of travel.

Figure 1 shows that *Avahi* also travelled further in each kilometer of travel by leaping (800 m compared to 667 m in *Lepilemur*), but normal climbing contributed 103 m to a kilometer of travel vs. 250 m in *Lepilemur*.

#### Height of observation

The GLM on the full dataset gave probabilities of <.01 for differences in heights of initial and terminal supports in leaping, climbing, walking, foliage-crossing, and frog-hopping. The mean height of observation was found to be clearly significantly different in the two species, *Avahi* being consistently found about a meter higher than *Lepilemur* (*Avahi* mean rank 645.59; *Lepilemur* mean rank 258.52; Mann-Whitney U = 101,366; Wilcoxon Rank Sum W = 248,519; Z = -9.7535; two-tailed P = .0000; Monte Carlo significance = .0000 for both two-tailed and one-tailed probabilities, 99% confidence interval .0000-.0005). A significant difference was maintained in leaping locomotion (*Avahi* mean rank 387.59; *Lepilemur* mean rank 276.86; Mann-Whitney U =

37,952; Wilcoxon Rank Sum W = 82,503; Z = -7.3529; two-tailed P = .0000; Monte Carlo significance = .0000 for both two-tailed and one-tailed probabilities, 99% confidence interval .0000-.0005). A significant difference was also found for climbing locomotion (*Avahi* mean rank 171.44; *Lepilemur* mean rank 111.08; Mann-Whitney U = 4,686.5; Wilcoxon Rank Sum W = 18,216.5; Z = -6.222; two-tailed P = .0000; Monte Carlo significance = .0000 for both two-tailed and one-tailed probabilities, 99% confidence interval .0000-.0005).

On the basis of ANOVAs of the full dataset, *Avahi* and *Lepilemur* both lose and gain more height in climbing than in leaping (Table 11), but *Avahi* appears to lose considerably more height when leaping than does *Lepilemur*; which loses less height in leaping than in any other locomotor mode. However, the true significance levels of multiple ANOVAs on the same dataset are likely to be cumulative, and even the probabilities of .00 or less can only be regarded as suggestive of a trend to difference.

#### Support orientation

From the 25% sample, a cross-tabulation of frequency of use of first vertical, angled, sloping, and horizontal supports showed *Lepilemur* used vertical first supports in 53.2% of cases, angles in 32.4% of cases, slopes in 9.45% of cases, and horizontals in 4.9% of cases while *Avahi* used vertical first supports in 42.8% of cases, angles in 29.4% of cases, slopes in 19.6% of cases, and horizontals in 8.2% of cases. The Pearson chi-square value was 28.11345, exact two-tail probability .00000. Phi and Cramer's V values were both .168, and the Monte Carlo estimate of significance was .0000, 99% confidence range .0000-.0005. Gamma was .22901, exact significance .00001. The results show a clearly significant species difference, but the relationship between species and first support orientation is not particularly strong. When leaping displacements were compared, the Pearson chi-square fell to 12.92681, exact two-tailed significance .00452. Gamma was .20224, exact significance .00296. Phi and Cramer's V values were .14313, exact significance .00452. In climbing, the Pearson chi-square was 9.14714,

TABLE 5. Descriptive statistics for the different locomotor modes in *Lepilemur edwardsi*

Locomotor mode	Diameter of first support, mean $\pm$ SE (N)	Diameter of second support, mean $\pm$ SE (N)	Height of first support, mean $\pm$ SE (N)	Height of second support, mean $\pm$ SE (N)	Horizontal distance travelled, mean $\pm$ SE (N)
Leap	3.733 $\pm$ 0.08 (1,177)	3.373 $\pm$ 0.89 (979)	5.018 $\pm$ 0.05 (1,188)	4.398 $\pm$ 0.7 (984)	1.229 $\pm$ 0.03
Climb	3.642 $\pm$ 0.13 (644)	3.635 $\pm$ 0.14 (615)	5.376 $\pm$ 0.08 (653)	5.15 $\pm$ 0.09 (629)	0.818 $\pm$ 0.04 (511)
Walk	2.707 $\pm$ 0.19 (157)	2.324 $\pm$ 0.17 (148)	5.817 $\pm$ 0.16 (162)	5.591 $\pm$ 0.19 (151)	0.709 $\pm$ 0.06 (151)
Foliage cross	3.290 $\pm$ 0.2 (82)	2.729 $\pm$ 0.4 (82)	5.263 $\pm$ 0.2 (82)	5.590 $\pm$ 0.19 (82)	0.293 $\pm$ 0.02 (81)
Cantilever	3.000 $\pm$ 0.1 (3)	2.667 $\pm$ 0.88 (3)	5.467 $\pm$ 0.88 (3)	6.033 $\pm$ 1.30 (3)	0.883 $\pm$ 0.32 (3)
Frog hop	5.231 $\pm$ 0.72 (39)	4.500 $\pm$ 0.69 (38)	5.283 $\pm$ 0.28 (39)	5.382 $\pm$ 0.35 (38)	0.765 $\pm$ 0.23 (34)
Kangaroo hop	3.800 $\pm$ 0.7 (25)	2.300 $\pm$ 0.4 (65)	5.620 $\pm$ 0.7 (15)	5.960 $\pm$ 0.6 (35)	0.480 $\pm$ 0.1 (65)
Other	2.750 $\pm$ 1.14 (10)	2.00 $\pm$ 0.00 (3)	6.858 $\pm$ 0.82 (10)	4.670 $\pm$ 1.2 (25)	0.500 $\pm$ 0.25 (3)
Run	4.000 $\pm$ 1.37 (14)	3.500 $\pm$ 0.79 (14)	6.364 $\pm$ 0.63 (14)	6.291 $\pm$ 0.55 (14)	1.129 $\pm$ 0.18 (14)
Ladder climb	4.500 $\pm$ 1.50 (2)	2.500 $\pm$ 0.50 (2)	5.250 $\pm$ 0.25 (2)	5.375 $\pm$ 0.88 (2)	0.300 (1)

exact two-tailed significance .02571; Gamma was .25668, exact significance .02902. Phi and Cramer's V values were .19986, exact probability .02571.

#### Support diameters

The GLM on the whole dataset had given probabilities of <.01 for species differences in the diameters of initial and terminal

supports in leaping, climbing and frog-hopping. From a 25% random sample, no significant differences were found, but for a 50% random sample there was an overall difference in means. Using a Mann Whitney U/Wilcoxon Rank Sum W test, *Lepilemur's* mean rank was 1,133.83, while *Avahi's* was 1,048.99 (U = 545,656.5; W = 1,193,747.5; Z = -3.1989; two-tailed P = .0014; Monte

TABLE 6. Descriptive statistics for the different locomotor modes in *Avahi occidentalis*

Locomotor mode	Diameter of first support, mean $\pm$ SE (N)	Diameter of second support, mean $\pm$ SE (N)	Height of first support, mean $\pm$ SE (N)	Height of second support, mean $\pm$ SE (N)	Horizontal distance travelled, mean $\pm$ SE (N)
Leap	3.308 $\pm$ 0.05 (1,514)	2.994 $\pm$ 0.06 (1,186)	6.103 $\pm$ 0.50 (1,527)	5.222 $\pm$ 0.07 (1,193)	1.361 $\pm$ 0.03 (1,164)
Climb	3.080 $\pm$ 0.12 (400)	3.062 $\pm$ 0.11 (398)	6.596 $\pm$ 0.10 (405)	6.160 $\pm$ 0.11 (401)	0.664 $\pm$ 0.05 (278)
Walk	2.436 $\pm$ 0.13 (141)	2.453 $\pm$ 0.14 (137)	7.026 $\pm$ 0.16 (145)	6.693 $\pm$ 0.21 (137)	0.742 $\pm$ 0.05 (135)
Foliage cross	2.539 $\pm$ 0.25 (39)	1.958 $\pm$ 0.25 (36)	7.600 $\pm$ 0.36 (40)	7.362 $\pm$ 0.41 (39)	0.385 $\pm$ 0.05 (39)
Cantilever	2.033 $\pm$ 0.29 (18)	1.889 $\pm$ 0.23 (18)	6.611 $\pm$ 0.56 (18)	6.983 $\pm$ 0.41 (18)	0.508 $\pm$ 0.06 (18)
Frog hop	3.171 $\pm$ 0.31 (25)	2.871 $\pm$ 0.25 (35)	6.537 $\pm$ 0.27 (35)	6.857 $\pm$ 0.27 (35)	0.747 $\pm$ 0.08 (33)
Kangaroo hop	3.267 $\pm$ 0.5 (9)	2.833 $\pm$ 0.47 (15)	6.013 $\pm$ 0.31 (15)	6.500 $\pm$ 0.32 (15)	0.660 $\pm$ 0.14 (15)
Other	1.032 $\pm$ 0.12 (19)	1.656 $\pm$ 0.33 (16)	7.326 $\pm$ 0.47 (19)	6.471 $\pm$ 0.78 (17)	0.571 $\pm$ 0.11 (12)
Run	2.596 $\pm$ 0.19 (47)	2.737 $\pm$ 0.21 (38)	6.447 $\pm$ 0.27 (47)	6.733 $\pm$ 0.27 (39)	0.925 $\pm$ 0.08 (38)
Ladder climb	2.750 $\pm$ 0.44 (52)	2.430 $\pm$ 0.23 (50)	6.500 $\pm$ 0.21 (55)	6.367 $\pm$ 0.22 (50)	0.535 $\pm$ 0.12 (10)



TABLE 7. Frequency (%) of use of the first supports of different orientation for each locomotor mode in *Lepilemur edwardsi*

Locomotor mode	N	Vertical (%)	Angled (%)	Oblique (%)	Horizontal (%)	Fork (%)	Foliage (%)
Leap	1,191	52.4	28.6	6.8	3.7	6.6	1.9
Climb	654	47.5	31	7.1	2.9	9.1	2.5
Walk	162	13.6	32.7	29	11.1	5.6	8
Foliage cross	82	29.6	39.5	14.8	1.2	12.3	2.5
Cantilever	3	33.3	66.7	0	0	0	0
Frog hop	40	41	38.5	7.7	0	12.8	0
Kangaroo hop	5	0	40	0	0	60	0
Other	11	27.3	36.4	0	18.2	9.1	9.1
Run	14	0	50	28.6	14.3	0	7.1
Ladder climb	2	0	0	0	100	0	0

TABLE 8. Frequency (%) of use of first supports of different orientation for each locomotor mode in *Avahi occidentalis*

Locomotor mode	N	Vertical (%)	Angled (%)	Oblique (%)	Horizontal (%)	Fork (%)	Foliage (%)
Leap	1,537	48.1	26.2	14.1	6.3	4.4	1
Climb	408	42.5	25.9	11.4	5.7	10.2	4.2
Walk	145	10.4	12.5	45.1	20.1	7.6	4.2
Foliage cross	40	32.5	30	17.5	10	2.5	7.5
Cantilever	37	8.6	37.1	31.4	17.1	5.7	0
Frog hop	15	6.7	73.3	13.3	0	6.7	0
Kangaroo hop	15	6.7	73.3	13.3	0	6.7	0
Other	19	0	5.3	47.4	36.8	5.3	5.3
Run	47	14.9	27.7	51.1	4.3	2.1	0
Ladder climb	55	12.7	9.1	43.6	25.5	3.6	5.5

TABLE 9. Frequency (%) of use of second supports of different orientation for each locomotor mode in *Lepilemur edwardsi*

Locomotor mode	N	Vertical (%)	Angled (%)	Oblique (%)	Horizontal (%)	Fork (%)	Foliage (%)
Leap	1,191	56.4	29.2	6.4	3.4	2.4	2.2
Climb	654	49.4	29.5	5.2	1.8	11.1	3
Walk	162	8.1	32.9	32.2	15.4	5.4	6
Foliage cross	82	37.8	34.1	12.2	6.1	1.2	7.4
Cantilever	3	100	0	0	0	0	0
Frog hop	40	37.5	33.3	11.1	2.8	11.1	0
Kangaroo hop	5	20	40	20	0	0	20
Other	11	0	66.7	33.3	0	0	0
Run	14	7.1	42.9	28.6	14.3	7.1	0
Ladder climb	2	0	100	0	0	0	0

Carlo probabilities .0016 (two-tailed; 99% confidence interval .0006–.0026) and .0008 (one-tailed; 99% CI .0001–.0015). A difference was sustained in leaping (mean ranks 703.16 and 647.4, respectively;  $U = 202,616.5$ ;  $W = 493,319.5$ ;  $Z = -2.6568$ ; Monte Carlo probabilities .0082 (two-tailed; 99% CI .0059–.0105) and .0042 (one-tailed; 99% CI .0025–.0059). A significant difference was not sustained in climbing however.

#### Length of displacements (bouts)

The GLM on the full dataset gave probabilities of <.01, <.01, and <.05 for the

significance of differences in bout length in leaping, climbing, and foliage-crossing, respectively, but on the basis of the 25% random sample no significant difference was found either overall or for individual locomotor modes. This also applied when the effective mechanical distance of leaps was calculated and compared (see below). However, a *t*-test on a 50% random sample gave a two-tailed equal-variance probability of .000 for overall means of 1.38 (*Lepilemur*) and 1.56 m (*Avahi*). A Mann-Whitney U/Wilcoxon Rank Sum W test on the same sample gave a mean rank of 872.85 and 994.31,

TABLE 10. Frequency (%) of use of second supports of different orientation for each locomotor mode in *Avahi occidentalis*

Locomotor mode	N	Vertical (%)	Angled (%)	Oblique (%)	Horizontal (%)	Fork (%)	Foliage (%)
Leap	1,537	51.9	29.1	13.1	3.3	1.7	0.8
Climb	408	55.9	24.1	5	4.2	7.3	3.4
Walk	145	2.3	9.2	51.5	33.1	3.8	0
Foliage cross	40	30.8	20.5	15.4	23.1	2.6	7.7
Cantilever	18	27.8	16.7	38.9	16.7	0	0
Frog hop	37	22.9	17.1	28.6	25.7	5.7	0
Kangaroo hop	15	33.3	33.3	33.3	0	0	0
Other	19	26.7	0	46.7	26.7	0	0
Run	47	2.6	23.1	66.7	7.7	0	0
Ladder climb	55	12	24	36	24	4	0

respectively ( $U = 380,444.5$ ;  $W = 752,397.5$ ;  $Z = -4.8813$ ; two-tailed asymptotic probability = .0000). A difference was sustained for leaping (mean ranks 435.75 [*Lepilemur*] and 494.64 [*Avahi*];  $U = 94,646.5$ ;  $W = 184,322.5$ ;  $Z = -3.3470$ ; two-tailed asymptotic probability = .0008); the Monte Carlo probability was .00007 (two-tailed) or .0004 (one-tailed), for which the 99% confidence intervals were .0000–.0014 and .0000–.0009, respectively. But for climbing, the differences in means were nonsignificant.

#### Relationships between the mechanical length of leaps, support diameter, and heights

There was no statistically significant difference between the mean mechanical length

of leaps in the two species. For *Lepilemur*, no significant differences were found either between the diameter of the takeoff support and the mechanical length of leaps. However, landing supports in leaps from class 6, with a mean diameter of 4.9 cm, differed at the .05 level from all shorter classes (means 2.5–3.9 cm), while those from group 8 (5.3 cm) differed from those in classes 1, 2, and 3 (means 3.9 cm and below). For *Avahi*, differences were found in the diameter of takeoff supports: again at the .05 level, the diameter of takeoff supports in length group 6 (mean 4.1 cm) was greater than that in groups 1, 2, and 3 (3.1 cm and below); the mean diameter of takeoff supports for leaps in group 5 (3.7 cm) and 4 (3.6 cm) also differed from those for leaps in groups 1 and 3. For landing

TABLE 11. Descriptive statistics of a one-way ANOVA comparing height lost and gained in each locomotor mode for number of bouts per mode (N), least mean square (LMS), standard error of LMS (SE LMS) and probability of difference between given mode mean (LMS) and means of other modes occurring randomly (P)

Locomotor mode	Height lost LMS	SE LMS	N	P	Height gained LMS	SE LMS	N	P
<i>Lepilemur edwardsi</i>								
Leap	<b>0.04</b>	0	681	0.00	<b>0.66</b>	0.0	193	0.00
Climb	<b>0.73</b>	0	353	0.00	<b>0.71</b>	0.0	263	0.00
Walk	<b>0.17</b>	0.1	101	0.02	<b>0.38</b>	0.1	44	0.00
Foliage cross	<b>0.1</b>	0.1	74	0.23	<b>0.30</b>	0.2	8	0.10
Cantilever	<b>0.3</b>	0.7	1	0.67	<b>1.00</b>	0.4	2	0.00
Frog hop	<b>0.04</b>	0.3	50	0.90	<b>0.51</b>	0.1	30	0.00
Kangaroo hop	<b>0.05</b>	0.5	2	0.92	<b>0.60</b>	0.3	3	0.04
Other	<b>0.15</b>	0.5	2	0.76	<b>0.30</b>	0.5	1	0.56
Run	<b>0.53</b>	0.2	9	0.02	<b>0.75</b>	0.2	5	0.00
Ladder-climb	<b>0.50</b>	0.7	1	0.48	<b>0.75</b>	0.5	1	0.1
<i>Avahi occidentalis</i>								
Leap	<b>0.48</b>	0.0	897	0.00	<b>0.64</b>	0.1	142	0.00
Climb	<b>0.84</b>	0.0	244	0.00	<b>0.79</b>	0.1	139	0.00
Walk	<b>0.13</b>	0.1	93	0.07	<b>0.27</b>	0.1	37	0.00
Foliage cross	<b>0.10</b>	0.1	36	0.07	<b>0.65</b>	0.4	2	0.11
Cantilever	<b>0.01</b>	0.2	14	0.94	<b>0.30</b>	0.3	3	0.36
Frog hop	<b>0.00</b>	0.2	10	1.00	<b>0.45</b>	0.1	2	0.00
Kangaroo hop	<b>0.58</b>	0.3	4	0.09	<b>0.87</b>	0.2	11	0.00
Other	<b>0.15</b>	0.2	12	0.44	<b>0.27</b>	0.3	3	0.42
Run	<b>0.29</b>	0.1	22	0.05	<b>0.41</b>	0.1	17	0.00
Ladder climb	<b>0.73</b>	0.1	24	0.00	<b>0.59</b>	0.1	26	0.00

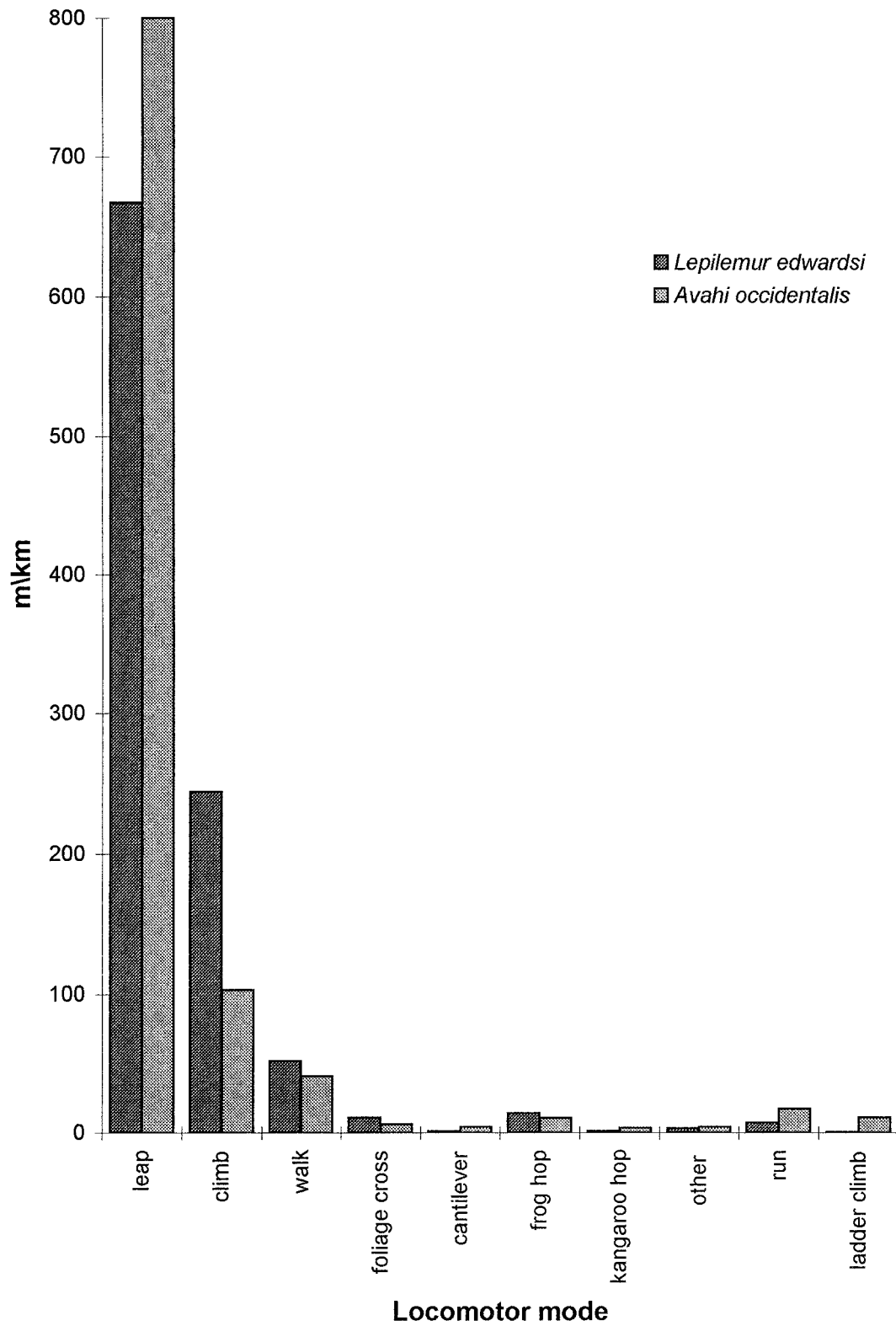


Fig. 1 Meters per kilometer travelled in each locomotor mode (N = 6,845).

supports, the mean diameter in leaps of length group 6 was 3.97, significantly different from groups 1 and 2 (3.04 and 3.14 cm, respectively). Leaps in classes 1 and 2 also differed from group 5 (3.68 cm), and the mean diameter for leaps in group 4 (3.82 m) differed from the means for groups 1, 2, and 3.

Differences also existed in the height lost or gained in leaps of different effective lengths, although the two are not independent of each other (see Method). Individually, at the .05 level, the mean gain in effective length groups 6, 5, and 4 was larger than in each of groups 1, 2, or 3, while the gain in group 3 differed from losses in groups 1 and 2.

From a sample including the whole dataset, height gain shows a weak positive correlation with the horizontal distance travelled in both species (*Lepilemur*: Pearson  $r = .2224$ ,  $P = .000$ ; Spearman  $r = .1252$ ,  $P = .014$ ; *Avahi*: Pearson  $r = .2304$ ,  $P = .000$ ; Spearman  $r = .2042$ ,  $P = .000$ ), the shortest leaps tending to lose most height, the longest to gain most height. The relationship in both cases is linear. However, the correlations between height change and leap length was not significant when a 25% random sample was tested.

## DISCUSSION

While both species are predominantly saltatory, frequencies (69.7% of *Avahi* vs. 55.8% of *Lepilemur* locomotor bouts), mean lengths (1.38 m in *Lepilemur* vs. 1.56 m in *Avahi*) and contributions to a kilometer of travel (800 m/km in *Avahi* vs. 667 in *Lepilemur*) suggest that *A. occidentalis* is behaviorally a somewhat more committed leaper than *L. edwardsi*. However, *L. edwardsi* loses much less height by leaping than does *Avahi*, which loses an average of nearly half a meter on each leap. In fact, *Lepilemur* loses less height in leaping than any other locomotor mode. These latter results suggest that while *Avahi* may be behaviorally more committed to leaping, *Lepilemur* is not inferior in its capacity to leap.

Comparable data are unfortunately rare. Although Dagosto (1995) uses only four locomotor categories (leaping, climbing, quadrup-

edalism, and other), her value of 89% leaping for *Propithecus diadema* seems remarkably high, compared with our figure of around 70% leaping for *Avahi*. However, her figure of 73% leaping for *Eulemur fulvus rufus* also exceeds both ours for *Avahi* and Crompton and Andau's (1986) figure for *Tarsius bancanus*. Further, Dagosto's figure of 55% leaping in the wet season and 48% in the dry season for *Varecia variegata* are both substantially higher than Britt's (1996) figure of 38% for *Varecia variegata* at Betampona in a two-category division (quadrupedalism and leaping), and her wet season figure for *Varecia* is actually larger than the overall figure of 53% for *Galago moholi* (Crompton, 1984). We must conclude that her field methods for bout sampling are not similar to our own and her figures not comparable.

Our findings on locomotor frequencies need to be interpreted with caution: knowing species improved prediction of locomotor frequencies by less than 10%. However, the absolute frequency of leaping seen in *A. occidentalis* is close to that of *T. bancanus* (66.1% [Crompton and Andau, 1986]) and *T. spectrum* (63% [MacKinnon and MacKinnon 1980]), and *A. occidentalis* covers considerably more of each kilometer of travel by leaping (Fig. 1). The value for *A. occidentalis* is very similar to that found in *T. bancanus* (882 m/km [Crompton and Andau, 1986]), while on the other hand the frequency and meter per kilometer values for leaping in *L. edwardsi* are closely similar to those for *G. moholi* (53%, 670 m/km [Crompton 1980, 1984]). However, the mean leap length of both lemurs (1.23 m for *L. edwardsi* and 1.51 m for *A. occidentalis*) is much greater than the 0.8 m mean leap of *G. moholi* and also greater than the 1.16 m recorded for *T. bancanus*. Despite the greater size of *Otolemur crassicaudatus*, its mean leap length was only 0.7 m (Crompton, 1984). The closest match is the 1.5–2.0 m figure of Charles-Dominique and Hladik (1971) for *Lepilemur leucopus*. In both *Avahi* and *Lepilemur*, normal climbing is the second commonest mode of locomotion, but here it is the frequency of climbing for *L. edwardsi* which resembles that seen for *T. bancanus*, while *A. occidentalis* in this respect is comparable to *G.*

*moholi*. The bout lengths for normal climbing in *Avahi* (0.67 m) and *Lepilemur* (0.71 m) are both much larger than in *Tarsius bancanus* (0.29 m).

In terms of support use, the raw data appear to show that both species have a strong affinity for vertical and angled first supports in leaping and climbing, and Ganzhorn (1993) has also suggested that these species use parts of the forest with vertical supports more frequently than expected by chance. *Lepilemur* was observed on vertical first supports in 42.5% of cases and *Avahi* in 37% of cases, while Nash's (in press) figures (including postural behavior) are equivalent to about 35% usage. Dagosto (1995) gives figures of 23–28% use of verticals for *Propithecus diadema* in a three-way division. Both species' utilization of verticals is much more than *Galago moholi*'s (16% [Crompton, 1984]) but much less than that of *Tarsius bancanus* (72.4% [Crompton and Andau, 1986]). Their use of verticals also seems less than that of *G. alleni* (73% in a three-category division [Charles-Dominique, 1977]) and *T. spectrum* (65% in a three-category division [McKinnon and McKinnon 1980]). While *Lepilemur* also ends leaping bouts more often on vertical supports than does *Avahi*, the reverse applies for climbing. However, one of us has shown (Warren, 1997) that the affinity for vertical and angled supports is not sustained in either species when support availability is taken into consideration. In fact, both species show a preference for oblique (sloping) and horizontal supports rather than verticals. *Avahi* shows the bigger preference for horizontals. Both species, however, show a strong preference for supports between 0.5 and 5 cm in diameter, as Nash (in press) also found for *L. leucopus* (her figures amount to 71% usage of supports of 5 cm or below), and *Avahi* shows the greater avoidance of the largest supports. In this respect, their support preferences are similar to those found by Niemitz (1984a,b) for *T. bancanus*, which used supports of 3–4 cm diameter 2.4 times as often as they occurred at his site, Semongok, in Sarawak.

While the statistical tests on a 25% random sample showed no significant difference in mean support diameter, those on the 50%

random sample and whole dataset did show a significant difference, *Avahi* using smaller-diameter supports than does *Lepilemur*.

Contrary to Ganzhorn (1988, 1989, 1992), our much larger sample shows that the 1 m difference in height both his and our studies discovered is clearly statistically significant. These values compare with his estimates of a much larger difference in mean heights: 6.2 m vs. 3.2 m at Perinet. In contrast, Harcourt's (1987, 1991) studies gave sleeping site heights of around 3 m for *A. laniger* at Ranomafana, which suggests but does not allow us to conclude that niche differentiation by stratum does take place when the two species are sympatric.

Ganzhorn (1993) suggests on the basis of a population densities in unlogged and lightly logged woodland that *Lepilemur* populations may be constrained by intertree distances. However, the mean leap length of both species in our study (1.5 m. for *Avahi*, 1.23 m for *Lepilemur*), although long compared to that of *Tarsius* and *Galago* species, is well below the mean intertree distance at Ampijoroa (2.55 m. [Warren, 1997]). In contrast, Niemitz (1984b) found that the mean intertree distance at his study site for *T. spectrum* was less than half the mean leap length of 1.16 m. Both *Avahi* and *Lepilemur* can leap well over 4 m. Both species appear to gain height on the longest leaps but lose height on the shortest. *Lepilemur* in particular loses little height by leaping. This suggests that it is the cost of longer leaps, not any mechanical inability to perform them, that is more likely to constrain our species and also suggests that both species would be constrained by intertree distances, *Avahi* no less than *Lepilemur*.

Despite the weakness of the difference in support diameters, support use and height of observation are related in a similar manner as they were in Crompton's (1984) comparison of *Galago moholi* and *Galago crassicaudatus*: the species found lower down uses larger and more vertical supports. However, unlike our present subjects, the two bushbabies were not sharing the same trees. But in reverse of Crompton's (1984) findings, in the present study the species that moves lower down leaps less often (and to a lesser extent



less far) but climbs more. Reduction in the amount of leaping may necessitate an increase in detours made by climbing up and down tree and sapling trunks.

In forceplate studies of leaping, Preuschoft (1985), Günther (1989), Demes and Günther (1989), and Günther et al. (1991) have found that landing forces are higher than takeoff forces, so that we might expect leaping animals to select landing supports of smaller diameter in relation to their body mass. Results of our study of the relationship of effective distance to support diameter shows that *Avahi* uses larger diameter supports both to take off from and to land on when the effective length of the leap is longer. *Lepilemur* uses larger supports to land on only when the effective length of the leap is greater. The use of larger diameter landing supports agrees with the findings of Crompton et al. (1993) for *Tarsius bancanus* and *Galago moholi* but disagrees with their finding for *Otolemur crassicaudatus*. This tends to support the argument of Crompton and colleagues (1993) that the long legs of specialist leapers, which land feet-first (as do *Lepilemur* and *Avahi*, *T. bancanus* and *G. moholi*) allow landing forces to be dissipated over a longer time duration, just as they allow takeoff forces to be applied over a longer time duration; thus, rigid landing supports are favored because they are more stable. It is the unspecialized leaper, landing forelimb-first, such as *G. crassicaudatus*, which avoids landing on rigid supports. Our finding that *Avahi* also appears to use larger supports to take off from agrees with Crompton and colleagues' (1993) result for *Galago moholi* but contrasts with their finding for *T. bancanus*. Both of the former pair thus appear to avoid energy loss to the substrate on takeoff. Demes and colleagues (1995) found that loss of energy to the takeoff support is more probable than energy return by rebound. *Tarsius* may not need to avoid such loss since its relative costs of locomotion are low compared to other prosimians we have studied (Warren and Crompton, in press b).

*L. edwardsi's* apparent indifference to energy loss to the substrate may perhaps be accounted for by its remarkably short nightly travel distances, combined with relatively long leaps. While surveyed point-to-point

distances are inevitably an underestimate of total travel distance, *L. edwardsi's* mean daily travel distance, about 343 m, represents only 278 typical leaps. Similarly, Charles-Dominique and Hladik's (1971) figure of only 270 m (from a single all-night follow) represents about 180 leaps. On the other hand *Avahi's* nightly distance of 1,175 m represents about 783 leaps; *T. bancanus's* 1,800 m nightly distance represents about 1,551 typical leaps (Crompton and Andau, 1987), and *G. moholi's* 1,440 m represents about 1,800 typical leaps (from Harcourt, 1980; Crompton, 1984). *Avahi* and *G. moholi* perhaps need to reduce energy losses, while *Tarsius* avoids this problem by being small (Warren and Crompton, in press b) and *Lepilemur* by the reduced activity levels found by Charles-Dominique and Hladik (1971) and Nash (in press). Further, Schmid and Ganzhorn (1996) have found that *Lepilemur ruficaudatus* has the lowest resting metabolic rate so far recorded for a folivorous mammal, and *Lepilemur* may thus save energy by reducing not only its locomotor energy budget but that for thermoregulation.

Ganzhorn (1993) has shown that, in terms of their favored food trees, resources for *Lepilemur* are more clumped than for *Avahi*. This would tend to suggest that ranging patterns we have observed for *Lepilemur* and *Avahi* at Ampijoroa are a reflection of the distribution of their preferred food rather than of social-behavioral factors. Ganzhorn (1992) has shown that, at Perinet, *A. laniger*, moving higher up, will encounter fewer leaves containing plant toxins, specifically alkaloids and tannins, than will *L. mustelinus*, since the undergrowth contains more species containing toxins. Further, our own observations of dietary behavior, as well as those of Razanahoera-Rakotomalalala (1981, 1988), indicate that *Avahi* shows much more discrimination in selection of leaves than *Lepilemur*, which eats by grasping a branch and consuming leaves indiscriminantly and almost frenziedly. Similarly, Nash (in press) found that *Lepilemur* "sits on what it eats and eats what it sits on" and feeds for a long period in one area before moving on. While dead leaves were generally avoided by *Lepilemur*, old leaves were commonly eaten, and at the end of the dry season even dying and dead leaves of *Tabemaemontana modesta*

(Apocynaceae) were seen to be taken. *Avahi*, however, would eat leaves only after close inspection, eating only one or two from a branch before looking for a new source. Flowering trees would be stripped of flowers by *Avahi* within two or three nights. *Lepilemur*, moving at a lower level than *Avahi* and eating leaves indiscriminantly, would be bound to take in more leaves containing tannins and alkaloids than *Avahi*, and indeed Ganzhorn (1992, 1993) has shown that, when *Avahi* are present, *Lepilemur* takes poorer quality foods. He interprets this as behavioral character displacement but notes that both Chivers and Hladik (1980) and Razanahoera-Rakotomalalala (1981, 1988) have noted differences in gut and dental morphology between the two genera, suggesting ample room for dietary niche differentiation. On the other hand, since *Lepilemur edwardsi* appears both to be less selective in its food than *Avahi occidentalis* and to use more clumped food resources, it may also be able to reduce the area which it has to search for food and conserve energy in this way.

### CONCLUSIONS

Thus, *Avahi occidentalis* and *Lepilemur edwardsi*, whilst showing a generally similar locomotor repertoire, differ in emphasis, especially with respect to stratum: *Avahi* is the more dedicated leaper, but it is *Lepilemur*; moving lower down, which both uses and encounters a greater number of vertical, large-diameter supports. The same forest is clearly being exploited in different ways by the two lemurs. We may surmise that locomotor behavior forms an important part of a mechanism for niche differentiation, where *Lepilemur* avoids competition with *Avahi* by exploiting plant species in the undergrowth which contain more toxins. In turn, this diet may so reduce the energy available to *Lepilemur* that its leaping locomotion has to be drastically curtailed. *Avahi*, on the other hand, consumes a richer but less ubiquitous new leaf and flower diet, which we propose necessitates that *Avahi* employs locomotion which allows it to exploit the canopy over a large daily range.

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### LITERATURE CITED

- Albignac R (1981a) Variabilité dans l'écologie de *Avahi laniger* (Lémurien nocturne de Madagascar). C. R. Acad. Sci. Paris 292:331–334.
- Albignac R (1981b) Lemurine social and territorial organization in a north-western malagasy forest. In AC Chiarelli and RS Corruccini (eds.): Primate Behavior and Sociology. Berlin: Springer-Verlag, pp. 25–29.
- Alexander RM (1991) Elastic mechanisms in primate locomotion. Z. Morphol. Anthropol. 78:315–320.
- Biewener A, Alexander RM, and Heglund NC (1981) Elastic strain energy in the hopping of kangaroo rats. J. Zool. 195:369–383.
- Boinski S (1989) The positional behavior and substrate use of squirrel monkeys: Ecological implications. J. Hum. Evol. 18:659–677.
- Britt A (1996) Environmental Influences on the Behavioural Ecology of the Black and White Ruffed Lemur (*Varecia variegata variegata* Kerr, 1792). Ph.D. dissertation The University of Liverpool.
- Charles-Dominique P (1977) Ecology and Behaviour of Nocturnal Prosimians. London: Duckworth.
- Charles-Dominique P, and Hladik CM (1971) Le *Lepilemur* du sud de Madagascar: Ecologie, alimentation et vie sociale. La Terre et la Vie 25:3–66.
- Chivers DJ, and Hladik CM (1980) Morphology of the gastrointestinal tract in primates. Comparisons with other mammals in relation to diet. J. Morphol. 166:337–386.
- Crompton RH (1980) A Leap in the Dark: Locomotor Behaviour and Ecology in *Galago senegalensis* and *Galago crassicaudatus*. Ph.D. dissertation, Harvard University, Cambridge, MA.
- Crompton RH (1983) Age differences in locomotion of two subtropical Galaginae. Primates 24:241–259.
- Crompton RH (1984) Foraging, habitat structure, and locomotion in two species of *Galago*. In PS Rodman and JGH Cant (eds.): Adaptations for Foraging in Nonhuman Primates. Contributions to an Organismal Biology of Prosimians, Monkeys and Apes, 1st ed. New York: Columbia University Press, pp. 73–111.
- Crompton RH (1989) Mechanisms for speciation in *Galago* and *Tarsius*. Hum. Evol. 4:106–116.
- Crompton RH, and Andau PM (1986) Locomotion and habitat utilization in free-ranging *Tarsius bancanus*: A preliminary report. Primates 27:337–355.
- Crompton RH, and Andau PM (1987) Ranging, activity rhythms, and sociality in free-ranging *Tarsius bancanus*: A preliminary report. Int. J. Primatol. 8:43–71.
- Crompton RH, Sellers WI, and Gunther MM (1993) Energetic efficiency and ecology as selective factors in the saltatory adaption of prosimian primates. Proc. R. Soc. Lond. [Biol.] 254:41–45.
- Dagosto M (1994) Testing positional behavior of Malagasy lemurs: A randomization approach. Am. J. Phys. Anthropol. 94:89–302.

- Dagosto M (1995) Seasonal variation in positional behavior of Malagasy lemurs. *Int. J. Primatol.* 16:807–833.
- Demes B, and Günther MM (1989) Biomechanics and allometric scaling in primate locomotion and morphology. *Folia Primatol.* 53:125–141.
- Demes B, Jungers WL, Gross TS, and Fleagle JG (1995) Kinetics of leaping primates: Influence of substrate orientation and compliance. *Am. J. Phys. Anthropol.* 96:419–429.
- Doran DM (1992) Comparison of instantaneous and locomotor bout sampling methods: A case study of adult male chimpanzee locomotor behavior and substrate use. *Am. J. Phys. Anthropol.* 89:85–99.
- Edgington ES (1987) *Randomization Tests*. New York: Marcel Dekker.
- Fleagle JG (1978) Locomotion, posture and habitat utilization in two sympatric Malaysian leaf monkeys (*Presbytis obscura* and *Presbytis melalophus*). In GG Montgomery (ed.): *Ecology of Arboreal Folivores*. Washington, DC: Smithsonian Institution Press, pp. 243–251.
- Fontaine R (1990) Positional behavior in Saimiri boliviensis and Ateles geoffroyi. *Am. J. Phys. Anthropol.* 82:485–508.
- Ganzhorn JU (1988) Food partitioning among malagasy primates. *Oecologia* 75:436–450.
- Ganzhorn JU (1989) Niche separation of seven lemur species in the eastern rainforest of Madagascar. *Oecologia* 79:279–286.
- Ganzhorn JU (1992) Leaf chemistry and the biomass of folivorous primates in a tropical forest: Test of a hypothesis. *Oecologia* 91:540–547.
- Ganzhorn JU (1993): Flexibility and constraints of *Lepilemur* ecology. In PM Kappeler and JU Ganzhorn (eds.): *Lemur Social Systems and Their Ecological Basis*. New York: Plenum Press, pp. 153–165.
- Gebo DL, and Chapman CA (1995) Positional behavior in five sympatric Old World monkeys. *Am. J. Phys. Anthropol.* 97:49–76.
- Günther MM (1989) Funktionsmorphologischen Untersuchungen zum Sprungverhalten an mehreren Halbaffenarten (*Galago moholi*, *Galago* (Otolemur) garnettii, *Lemur catta*). Ph.D. dissertation Freie Universität Berlin.
- Günther MM, Ishida H, Kumakura H, and Nakano Y (1991) The jump as a fast mode of locomotion in arboreal and terrestrial biotopes. *Z. Morphol. Anthropol.* 78:341–372.
- Harcourt CS (1980) Behavioural Adaptations in South African Galagos. M.Sc. thesis, University of Witwatersrand, Johannesburg.
- Harcourt CS (1987) Ecology and behaviour of *Avahi laniger*. *Int. J. Primatol.* 8:501.
- Harcourt CS (1991) Diet and behaviour of a nocturnal lemur, *Avahi laniger*, in the wild. *J. Zool. Lond.* 223:667–674.
- Hladik CM (1980) The dry forest of the west coast of Madagascar: Climate, phenology and food available for prosimians. In P Charles-Dominique, HM Cooper, Hladik A, Hladik CM, Pages E, Pariente GF, Pether-Rousseaux A, Pether JJ, and Schilling A (eds.) *Nocturnal Malagasy Primates: Ecology, Physiology and Behaviour*. New York: Academic Press, pp. 3–40.
- Hutchinson GE (1957) Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* 22:415–427.
- Kay RF (1984) On the use of anatomical features to infer foraging behavior in extinct primates. In: RS Rodman and JGH Cant (eds.): *Adaptation for Foraging in Non-Human Primates*. New York: Columbia University Press, pp. 21–33.
- MacKinnon J, and MacKinnon K (1980) The behaviour of wild spectral tarsiers. *Int. J. Primatol.* 1:361–379.
- Marly BFJ (1991) *Randomization and Monte Carlo Methods in Biology*. New York: Chapman and Hall.
- Martin RD (1990) *Primate Origins and Evolution*. London: Chapman and Hall.
- Milliken GA, and Johnson DE (1992) *Analysis of Messy Data*, 2nd ed., Vol. 1. New York: Chapman and Hall.
- Nash LT (in press) Vertical clingers and sleepers: Seasonal influences on the activities and substrate use of *Lepilemur leucopus* at Beza Mahafaly Special Reserve Madagascar. *Folia Primatol.*
- Nash LT, Iwaniec UT, and Schoeninger MT (1995) Diet selectivity among three prosimian species: Stable isotopes as monitors. *Am. J. Phys. Anthropol. Suppl.* 20:159 (abstract).
- Niemitz C (1984a) Locomotion and posture of *Tarsius bancanus*. In C Niemitz (ed.): *Biology of Tarsiers*. Stuttgart: Fischer, pp. 191–225.
- Niemitz C (1984b) Activity rhythms and use of space in semi-wild Bornean tarsiers, with remarks on wild spectral tarsiers. In C Niemitz (ed.): *Biology of Tarsiers*. Stuttgart and New York: Gustav Fischer, pp. 85–115.
- Pianka ER (1974) *Evolutionary Ecology*. New York: Harper and Row.
- Preuschoft H (1985) On the quality and magnitude of mechanical stress in the locomotor system during rapid movements. *Z. Morphol. Anthropol.* 75:245–262.
- Ramangason GS (1986) Analyse de la structure horizontale et verticale de la forêt sèche d'Ampijoroa. Troisième cycle thesis, Université de Madagascar, Antananarivo.
- Ramangason GS (1988) Flore et végétation de la forêt d'Ampijoroa. In L Rakotovo, V Barre, and J Sayer (eds.): *L'équilibre des écosystèmes forestiers à Madagascar: Actes d'un séminaire international*. Gland, Switzerland: IUCN, pp. 130–137.
- Razanahoera-Rakotomalala M (1981) Les adaptations alimentaires comparées de deux lémuriens folivores sympatriques: *Avahi*, Jourdan 1834, *Lepilemur*. I. Geoffroy, 1851. Ph.D. dissertation, University of Madagascar, Antananarivo.
- Razanahoera-Rakotomalala M (1988) Comportement alimentaire de deux espèces sympatriques dans la forêt d'Ankarafantsika (nord-ouest de Madagascar): *Lepilemur edwardsi* et *Avahi laniger* (Lémuriens nocturnes). In L Rakotovo and V Barre (eds.): *L'équilibre des écosystèmes forestiers à Madagascar: Actes d'un séminaire internationale*. Gland, Switzerland: IUCN, pp. 96–99.
- Russell RJ (1975) The Behavior Ecology and Environmental Physiology of a Nocturnal Primate *Lepilemur mustelinus*. Ph.D. dissertation, Duke University, Durham, NC.
- Schmid J, and Ganzhorn J (1996) Resting metabolic rates of *Lepilemur mustelinus ruficaudatus*. *Am. J. Primatol.* 3:169–174.
- Walker A (1979) Prosimian locomotor behaviour. In: GA Doyle and RD Martin (eds.): *The Study of Prosimian Behaviour*. London: Academic Press, pp. 543–464.
- Warren RD (1997) Habitat use and support preference of two free-ranging saltatory lemurs (*Lepilemur edwardsi* and *Avahi occidentalis*). *J. Zool. Lond.* 241:325–341.
- Warren RD, and Crompton RH (in press a) A comparative study of the ranging behaviour, activity rhythms and sociality of *Lepilemur edwardsi* and *Avahi occidentalis* at Ampijoroa, Madagascar. *J. Zool.*
- Warren RD, and Crompton RH (in press b) Diet, body size and the energy costs of locomotion in saltatory primates. *Folia Primatol.*